Proceedings of the Iowa Academy of Science

Volume 55 | Annual Issue Article 29

1948

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The genus Adiantum has few northern members but includes over a hundred tropical and subtropical species. Our chief northern representative, *A. pedatum,* ranges from Georgia to Nova Scotia, westward to the Pacific and north to Alaska. The other common temperate species, *A. capillus-veneris,* widespread in tropical and subtropical areas, is found chiefly in the southern part of the United States with limited northward extensions. While these two species overlap somewhat in their major distribution they belong to different geographical areas, but are similarly influenced by local conditions of substrate and habitat.

The extensive paper on chlorenchyma by Haberlandt (1882) included brief reference to the peculiar upper epidermal cells in *A. trapeziformae* L. He noted and figured the inward lobings of these cells and referred to them as a form of "armpalisade." Soon after several northern European botanists published on the leaf structure of their ferns and noted this unusual epidermal expression in additional species of *Adiantum* and for species of other genera of the Polypodiaceae. Since no one of the earlier writers gave special attention to these epidermal specializations and later workers have not emphasized this type of chlorenchyma the situation invites present attention. The writer has in press a paper dealing with the foliar organization of *A. pedatum* which includes references to earlier papers as well as results of a comparative survey of sixteen tropical and subtropical species of *Adiantum* secured from greenhouses (Wylie, 1948). While a few of the latter are horticultural forms, the list includes several good species and affords some information about members of this genus that are of tropical origin.

This previous paper on *A. pedatum* showed that while its leaves are always thin they vary considerably in structure not only among plants from different habitats but within the limits of a single pinnule. The chlorophyll bearing epidermal layers always contribute a major portion of the tissue between veins and cells of the upper epidermis always have proliferations of the inner face which border upon extensive subdermal intercellular spaces. There are only one or two layers of mesophyll and limited portions of all leaves examined had no interior tissue, leaving the epidermal layers in direct contact. Protuberances from the inner side of the upper epidermal cells extend across these spaces to contact the upper mesophyll or the lower epidermis if mesophyll is locally lacking. The epidermal layers expose the greater area of cell surface upon intercellular space and consequently they suffer the chief transpiration loss. Both epidermal layers have favorable vascular relations since they always contact directly either the endodermis or cells of the adjacent border paren-

chyma. This pattern of organization suggests that the covering layers doubtless aid materially with translocation and obviously provide most of the mechanical support for the wide areas between veins. It was not anticipated that a leaf structure so similar to that of the northern *A. pedatum* would be found among the species of tropical origin but three-fourths of the ones reviewed had a nearly identical pattern. These, in the paper noted (Wylie, 1948) are conveniently referred to as the *pedatum* group while the remaining members, including *A. trapeziforme,* are termed the *trapeziforme* group. The present paper deals more extensively with *A. capillus-veneris,* which was mentioned briefly in the earlier paper. Findings for this species will be compared to those for *A. pedatum* as well as with the tropical forms noted above.

Much of the material on *A. capillus-veneris* was secured through the courtesy of Dr. Henry S. Conard by whom it was collected in southern Missouri during the early autumn of 1947. Pinnules were killed in FAA and sectioned in both transverse and paradermal planes, usually 12μ thick but some 15μ in thickness. In addition. entire pinnules were mounted for study as noted below. All drawings were made x 985 using a Leitz Edinger drawing apparatus and were reduced two-thirds in reproduction.

RESULTS

Comparing the leaves of *A. capillus-veneris* and *A. pedatum,* the major differences noted by manuals relate to the rachis, pinnae and especially the form and position of pinnules. In the latter species the pinnules are short stalked obliquely oblong and entire on the lower margin from which all veins proceed. In *A. capillus-veneris* the pinnules are longer stalked, less compactly united into pinnae, often somewhat wedge shaped with branching veins fanning out from the base. In *A. pedatum* the pinnules have clefts only on the upper margin, while those of the other species have rounded or elongated lobes which are more freely and irregularly incised. In neither is there a mid-rib and in both the veins divide dichotomously with branches curving above forks to take nearly parallel trends.

The leaf structure of *A. capillus-veneris* conforms closely to the pattern described for *A. pedatum* but there are numerous differences, in part quantative, which are not apparent in the living material. Blade thickness in both is influenced by the amount of mesophyll present but there are marked differences between plants and likewise within the limits of a single pinnule. Marginal and terminal

DESCRIPTION OF FIGURES

Figs. 1-8. Leaf structure of *Adiantum capillus-veneris* L. Figs. 1, 2. Cross sections through portions of pinnule having two layers of mesophyll; Figs. 3, 4. through parts with one layer of mesophyll. Fig. 5. Portion of a paradermal section through the mesophyll, showing elongated cells and meshes formed by lateral branches. Figs. 6-8. Sections through areas having no mesophyll, leaving the epidermal layers in contact.

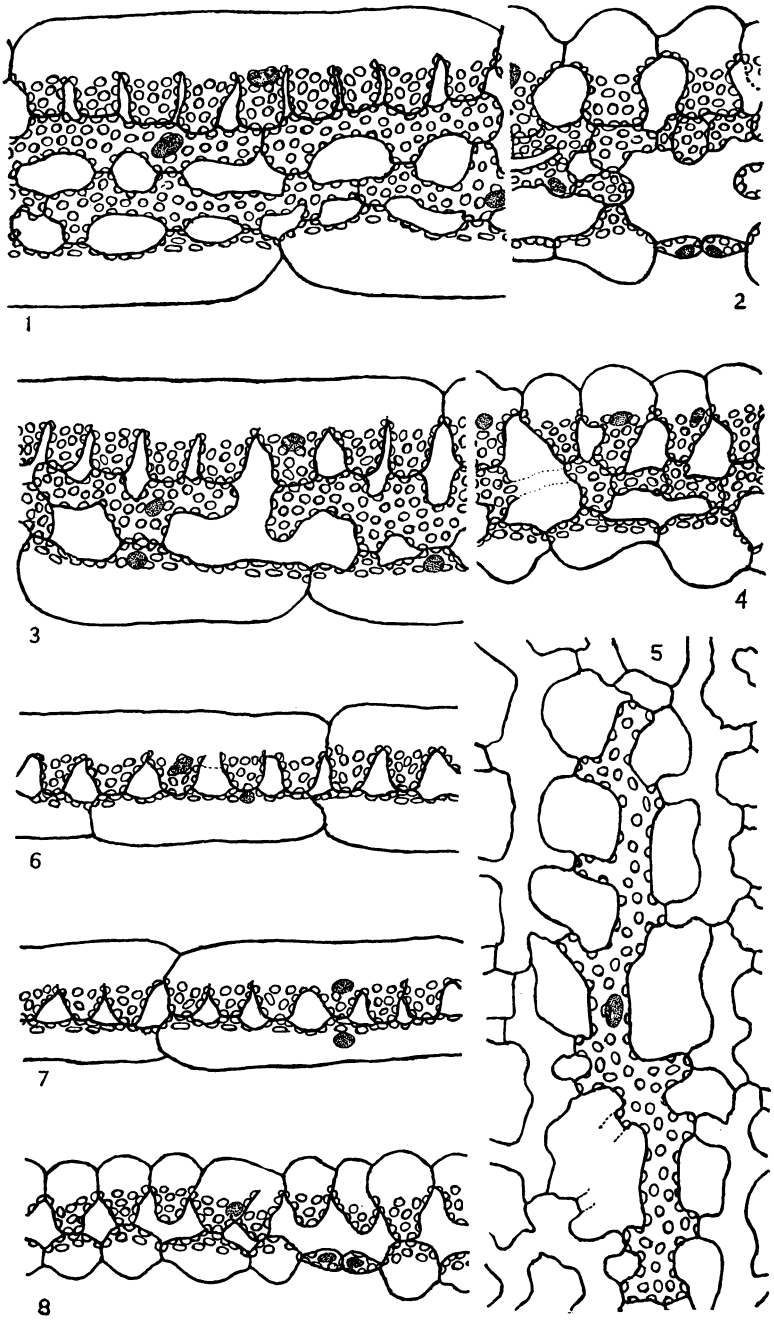

PLATE I

portions are thinner and there is reduced thickness between the widely separated vascular bundles. However blade thickness in *A. capillus-veneris* averaged (in the material studied) considerably greater. Measurements for a number of leaves from different plants gave for *A. capillus-veneris* a mean blade thickness: with two mesophyll layers, 120μ; one layer, 98μ; and for parts without mesophyll, 51μ. This is considerably more than the corresponding measurements for *A. pedatum* which were: with two layers of mesophyll, 64μ; one layer, 52μ; and no mesophyll, 32μ. In both species the third layer of mesophyll, when present, is restricted to the vein margin; no instance was noted where it spread out appreciably from the bundle.

Since the *epidermis* has a dominant place in the organization of the leaf in *Adiantum,* these layers will be taken up first. In both species the cells of the upper layer are fairly uniform in shape and are elongated parallel with the veins. They are separated by narrow lateral walls and have both inner and outer faces strongly convex. This gives their cells, seen in cross sections, a rounded form except for the appendages on the inner face (Figs. 2, 4, 8). The surface view shows elongated cells with sinuous lateral walls which are somewhat lobed in the plane of the blade; there is a tendency to alternate these lobings which results in a cell of fairly uniform width. Those of the upper epidermis average about 180μ in length, with many over 200μ long.

The lower epidermis, which carries all the stomata, displays much greater variety of cell size, shape and thickness. They are often irregularly lobed laterally or even branched and from thin cell margins may thicken abruptly to 50μ (Figs. 2, 4, 8). Cross sections of cells or cell lobes are roughly circular in form but cuts obliquely through cells often show highly irregular shapes. The mean thickness for cells of this layer was about 32μ but with marked differences over the area of a single cell because of their outer bulges. A feature noted only for deeply shaded foliage of other species was the frequent presence of chloroplasts along the outer walls of lower epidermal cells of *A. capillus-veneris* though most of them were closely packed along the inner walls of the same cells.

As discussed in the earlier paper there are always conspicuous subdermal intercellular spaces in these leaves. Cavities in the lower side of the blade are usually larger and correspond to spaces usually present in broader leaves of other vascular plants. But the marked development of such space systems beneath the upper epidermis is in striking contrast to the normal leaf pattern. This, as will be shown later, occurs in many of the Polypodiaceae having chloroplasts in the upper epidermal layer. However, the thicker leaves of the *trapeziforme* group, which have more mesophyll, had much smaller subdermal spaces. Evidently the development of these spaces in the upper side of the leaf is related to the possession of epidermal chlorenchyma, which necessitates, for land plants, exposed cell surface for gaseous exchange.

The protuberances from the inner face of the epidermal cells were larger in *A. capillus-veneris* than in any other species examined (Figs. 1-4). This results also in fewer papillae per given length of cell and per given area. In *A. capillus-veneris* they averaged 1850 per mm2 while in *A. pedatum* the average was 2800. The mean length of papillae for *A. capillus-veneris* was 25μ with a width of 21μ. Papillae near the ends of cells as well as the one nearest the center tend to be considerably larger and this difference is quite obvious in sections. In this species the lateral surface exposed by the papillae was over three times the area of the pinnule. When to this is added the free surface of the inner side of the upper epidermal cells it gave a total surface for gaseous exchange, as well as transpiration, that was about four times the area of the pinnule.

The inner face of the lower epidermis, while somewhat irregular, bears no specialized papillae though there are conical extensions at wide intervals where it meets the mesophyll. Due to the convexity of these cells they expose upon intercellular space an area probably one and one-half times the area of the blade. Together, the epidermal layers have an inner free surface of at least five times the area of the pinnule. Because their outer surface is also considerably increased by the regular convexity of outer walls, this area, though protected in some degree, likewise adds to the transpiration loss from the epidermis. There must be fairly ready supply to their cells and a probable route of transfer would be from veins to and through the epidermal layers.

The *mesophyll* of *Adiantum capillus-veneris,* like others of the *pedatum* group, consists usually of one or two layers (Figs. 1-4). If a third layer is locally represented, it lies in the vein margins. Mesophyll cells are always elongated parallel to the trend of the adjacent epidermal cells; they are cylindric in form, with numerous branches in the plane of the blade, which are cross ties or may unite with others to form a series of meshes between cells (Fig. 5). When two layers of mesophyll are present the cells of the upper are of greater diameter, have shorter branches and smaller meshes. If a single mesophyll, its cells are often undulating when seen in cross sections of the leaf (Figs. 3-4). Between contacts with upper papillae its cells usually curve downward; opposite contacts with the lower epidermis it may have nearly vertical branches or segments (Fig. 3). Meshes of the lower, or of a single mesophyll layer, are larger than those of the upper layer.

Surveys using paradermal sections showed a fairly distinctive cell length for different mesophyll layers. With two layers of sponge present the upper had an average cell length of 116μ and the lower 220μ, while for parts with a single layer the cell length averaged 133μ.

The mesophyll is highly porous; for portions of the pinnule with two layers of cells those of the upper averaged 19μ in diameter and about 40% of this stratum consisted of intercellular space, while the lower layer had cells 14μ in diameter and about 50% of

the volume occupied was space. With but a single layer of sponge present the cell diameter was 17.5μ and about 45% of the volume was intercellular space.

Because the epidermal layers are much thicker and are continuous they contribute about 77% of the total tissue-mass for portions of the blade with two layers of mesophyll and 90% where there is but one layer of sponge. For areas having no mesophyll the epidermal layers become the blade, 100%.

Of considerable interest is the lack of mesophyll over portions of these pinnules as recorded previously for the *pedatum* series (Figs. 6-8). All pinnules of *A. capillus-veneris* that were examined had certain distal and lateral areas without mesophyll aggregating from 2-5% of the total area; leaves of deeply shaded places would doubtless have greater proportions, as found in *A. pedatum*. While these areas are green and inconspicuous in the living leaf they show quite plainly if fresh pinnules are put first into 95% alcohol until the chlorophyll has been dissolved then mounted in water. Under low powers of compound microscopes the areas that have no sponge show quite clearly and under higher power may, by focusing, be found to consist of the epidermal layers only. Quite naturally this unusual feature is of significance to any interested in foliar organization. In considerable degree the covering layers of these ferns serve in various ways and have a dominant place both morphologically and physiologically and of course where mesophyll is locally lacking they represent the blade.

All *veins* are small and an endodermis is regularly present, but in *A. capillus-veneris* the border parenchyma is better developed and seldom spreads out laterally. It may consist of a complete ring of cells, elongated or circular in cross section. Often, however, this investment is interrupted above or below by the fiber cells of the epidermis which tend to be pressed against the bundle. In others, normal or slightly modified epidermal cells contact the endodermis and form a segment of its investment. While the vascular pattern leading to the pinnules is quite different for these two species the smaller distributive veins within the blade are similar in arrangement and structure. In both there may be direct contact between epidermis and endodermis but this is less frequent here than in *A. pedatum*. However the alternative, contact with the border parenchyma, leaves but a single cell layer between epidermis and endodermis.

Examination of mounted pinnules of these two species showed certain minor differences. The veins in *A. capillus-veneris* seem to extend to the margin of the pinnule. Actually the xylem terminates at varying distances from the edge, but elongated epidermal and mesophyll cells simulate veins continuing to the hem of the blade. In *A. pedatum* there is a similar variation in the distance between tips of xylem strands at the edge of the blade but there remains a clear zone along the margin of the pinnule, much narrowed of course past the ends of veins. The distance between outermost tracheid

and hem varied so widely among pinnules of both species that no significant difference could be established. There remains, however, the apparent difference as to termini of veins in *A. capillus-veneris*.

While the structure of the marginal hem of these pinnules is similar for both, there are some differences in details. The hem of *A. capillus-veneris* consists of fewer thick walled cells which are circular in cross section and united laterally to cover the edge and is usually but one cell think. In *A. pedatum* the border cells are smaller, usually flattened or angled in cross section and may be irregularly massed into a structure that is several cells in depth. The binder cells of this species are so tough that with ordinary methods they may not cut when sectioned in paraffin but tear out when the knife strikes them. The width of the hem is also slightly greater in this species, 17μ compared with 15μ, measured in the plane of the blade.

One further difference that seems quite uniform is the presence of short cells in the hem of *A. capillus-veneris* opposite the elongated cells at tips of veins. The clear sclerenchyma cells of the hem are divided into short segments that have their end walls in line with the cells of the pseudo-vein. While there may be shorter cells opposite the tips of veins in *A. pedatum,* they are generally oblique so do not show clearly. Unfortunately all three of these minor distinctions may be appreciated only under low power of a compound microscope and are not apparent in the green or dried leaf.

In evaluating their *vascularization* measurements were made between the edges of adjacent veins. All species of *Adiantum* have wide separation of veins compared with the intervascular spacing in dicotyledon leaves. Interior portions of the pinnules have wider vein spacing than basal and terminal parts; for comparative purposes measurements were taken from interior and subterminal areas. The mean vein spacing for seven pinnules of *A. capillus-veneris* was 713μ while that reported earlier for *A. pedatum* was 586μ. This is four or five times the intervascular intervals reported for considerable groups of dicotyledons.

As discussed in the previous paper this local parallelism of veins in these ferns necessitates translocation chiefly at right angles to the trend of the veins. While this resembles somewhat the situation in most monocotyledons it is basically different from that in typical dicotyledons. In their leaves the minor veins branch freely in the plane of the blade so that local areas of mesophyll are served by radial translocation rather than primarily lateral movement between veins.

DISCUSSION AND SUMMARY

Leaves of this type offer numerous contrasts to the normal foliage of dicotyledons. Perhaps the most outstanding difference is the large size of many individual fern leaves. In this respect Adiantum shares in the macrophyllous habit so conspicuous among the Filicineae. This characteristic, as in Monocotyledons, is basically associated with

non-woody stems that do not branch freely and consequently have fewer growing points and a limited quota of leaves per plant. In addition, the ferns under study have subterranean stems which situation adds to the responsibilities of their leaves if they are to achieve much chlorenchyma. Also there are numerous structural differences between leaves of these two major groups. Among these are the possession by *Adiantum* of an endodermis, subdermal intercellular spaces in the upper side of the pinnules, reduced mesophyll. elongated sponge cells, wider separation of veins and a different pattern of vein distribution in the pinnules. Perhaps the most striking organizational feature is their emphasis upon the epidermis which has a structural and functional dominance unusual among vascular plants.

These two species of *Adiantum* are our chief representatives of a prominent genus that is preponderantly tropical in its spread. *A. pedatum* is definitely northern while *A. capillus-veneris* is tropical, subtropical and southern, with limited expression northward. Both are peculiarly restricted within the limits of their range by local conditions of substrate and habitat. Their leaves differ in type of rachis, form of pinnae, shape and insertion of pinnules and in pattern of vascular supply.

The present study of their leaves reveals several structural differences not apparent in living or dried material. *A capillus-veneris* has thicker pinnules and slightly more mesophyll due to a greater proportion having two layers of sponge. Its epidermal layers are thicker and the papillae on the under side of upper epidermal cells are much larger though fewer per unit area. Cells of the lower epidermis may have some chloroplasts along the outer wall, though regularly closely packed also against the inner wall. Veins are more widely spaced in this species. The veins appear to extend to the marginal hem of the pinnule which has usually fewer and larger cells than in the *A. pedatum.*

In spite of these numerous macroscopic and miscroscopic differences the leaves of these two species are much alike and have essentially the same pattern or organization. Common characteristics include the possession of chloroplasts in both epidermal layers, which not only support mechanically the areas between veins but also contribute the fiber-like cells above and beneath the bundles. These covering layers likewise provide the major area of moist cell wall exposed upon intercellular space, favoring gaseous exchange, and as a consequence suffer the greater transpiration loss. Much of the photosynthate originates within the epidermal cells and these layers undoubtedly aid in translocation between veins. The mesophyll in these species is limited to one or two layers but varies within each pinnule and both species have portions of the blade without mesophyll. Their vascular bundles are much alike, but those in *A. capillus-veneris* have a better developed border parenchyma. All bundles are small and in both species the epidermal layers contact either the endodermis or the border parenchyma. The spacing between veins

averages somewhat greater in *A. capillus-veneris,* with a mean separation of 713μ, while that for *A. pedatum* was 586μ.

These *Adiantum* ferns, especially those of the *pedatum* group, have achieved a fairly distinctive type of foliar organization. Their outstanding features are thin blades, due mainly to reduced mesophyll, and a dominant epidermis which carries a major portion of the chloroplasts and functions in various ways. While this type is doubtless a product of moist and sheltered habitats, these conditions have not resulted in a stereotyped pattern. A surprising feature is their range in foliar structure; members of these species have tissue variations that quantitatively rival the well known differences of "sun-shade" foliage in dictyledons. A noteworthy feature is the prevalence of this uniform pattern among species of the *pedatum* group from tropical, subtropical, and temperate climates.

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